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A magnificent expanse of grassland occupied the central part of North America before the coming of the white man. This paper is the result of a continuous investigation which began in 1916 of a large portion of this prairie. The area of most intensive study included approximately the western third of Iowa and the eastern third of Nebraska. The advent of the great drought of 1933 to 1940 offered an exceptional opportunity to ascertain the responses of native plants to extremely adverse conditions. The role played by rhizomes of grasses in endurance of drought and frequently their recovery from it was very impressive. Indeed only then did the great importance of the part of the prairie in the upper four inches of soil—the prairie sod—become clear. Hence a special study was made in 1961-62 on this portion of prairie vegetation.

The rhizomes of most prairie plants are relatively shallow and confined to the upper four to five inches of soil. They have a comparatively long life, perhaps many years. Plant parts in prairie sod are protected from sudden and extreme changes in temperature. They are scarcely harmed by frost or severe cold of winter, driving hail, tornadoes, or prairie fires. They endure ravages by grasshoppers and greatly prolonged drought. To prairie sod, only the plow is lethal.

The ability to adjust itself to the environment by various degrees of tillering accounts in a large measure for the successful occupation of more of the earth's surface by grass than by any other life form. The development of an extensive system of rhizomes not only enables grasses to spread widely into open spaces but also to invade underground and place new growing points between or beneath other plants, which are then often replaced. Moreover, rhizomes afford an excellent place for food accumulation and some retain life even after above-ground parts have long since disappeared and root systems have been greatly weakened or died.

Translocation and storage of reserves in the underground organs of grasses has been well summarized as follows; "Certain carbohydrates (mainly sugars, fructosans, dextrins and starch) have been shown to be the principal reserve substances in grasses. These materials are elaborated by the leaves in excess after flowering, and are subsequently translocated to the roots and rhizomes, where they are stored to be drawn in the following spring for the production of new top growth. Nitrogen and mineral elements (though not being reserves in the true sense of the word but merely nutrients) are likewise translocated in autumn from the aerial parts to the underground system where they are stored over winter" (Weinmann, 1948).

Few studies have been made upon the rhizomes or other plant parts in prairie sod, although Hitchcock (1899, 1900) gave general descriptions and a classification of the subterranean organs of several species of plants from the vicinity of Manhattan, Kansas. A notable exception is the excellent study by Mueller (1941). She traced the development of the rhizomes of several prairie grasses and forbs from seedlings to the adult stage, and thus through a complete annual cycle. Rate of vegetative spread was also ascertained.

In the present study, following Hayden (1919, 1934), Brenchley (1920), and Mueller (1941), a rhizome is considered as any somewhat uniformly thickened underground stem, regardless of its position in the sod. Names of grasses are according to Hitchcock and Chase (1950).

Composition of Prairie Sod

Samples of sod were taken in southeastern Nebraska and adjacent Iowa in spring and summer of 1961 and 1962. The soil was washed away and roots were separated from the network of rhizomes which was then described, divided into parts, and the length of each rhizome measured. Finally the air-dry rhizomes were weighed. Sod formed by the most abundant grasses of

lowlands and lower hillsides will be described first. Then the bunch grasses and others of upland drier sites will be examined.

Big bluestem

A representative block of the underground parts of big bluestem *(Andropogon gerardi)* is shown in Figure 1. It has an area

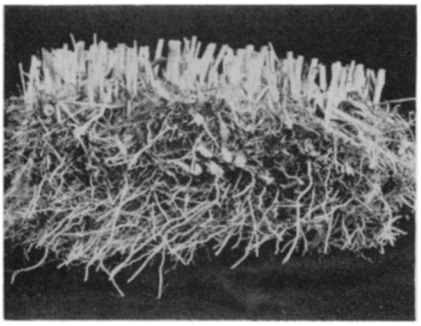

FIGURE 1. Sod formed by big bluestem includes stem bases, rhizomes and roots.

of about one square foot and over a period of three years developed from a centrally placed planting of ten seedlings. Conditions favorable to growth in a prairie environment were maintained. By tillering and development of rhizomes a characteristic sod was formed. Stems are normally about a centimeter apart, even in the densest sod they average less than one per square centimeter. The woody stem bases occupy the surface 1.5 inches of soil. They are five to eight millimeters in diameter. Within the block of sod there is a close network of coarse, gnarled, much-branched and intricately interwoven rhizomes. Many had extended beyond the area of the block and were cut off (light spots) in removing it from the soil.

Examination of a typical sample of sod from prairie revealed that the rhizomes are usually three to nine millimeters in diameter and often less than a foot long. They are normally crooked and well supplied with short branches. For example, one rhizome about eight inches long pursued a zigzag course and gave rise to ten short branches. There were 15 thickened stem bases in the sample, all of which were connected. These compact knotty bases gave rise to numerous coarse roots; many others arose from the rhizomes. This coarse and compacted system occurred mostly between one and three inches in depth.

Figure 2 illustrates the dense clumps of compacted rhizomes and stem bases which scarcely permitted the light to penetrate. Rhizomes appear to have a very long life since dead ones were rare in this and most of the numerous samples of various grasses. When they were separated and measured a total length of 61 feet of rhizomes per square foot of sod was found. When freed from roots and air dried, their weight was 105 grams. A second sample from another prairie yielded a total length of rhizomes of 59 feet.

The larger, densely compacted rhizomes from a somewhat wetter area in another prairie formed a dense mat about two inches thick, two to four inches below the soil surface. The intertwined tough roots were often three mm thick. They occurred at the rate of 650 per square foot (Weaver 1958). Total length of rhizomes per unit area was 53 feet. A final square foot sample from a flood plain yielded 100 grams of rhizomes from a length of 50 feet.

The average length of rhizomes of 55 feet per square foot of bluestem sod, indicates that an acre of this grass might contain more than 400 miles of rhizomes (Figure 3). The tensile strength of individual rhizomes three to four mm in diameter was found to vary but little. They broke only under a pull of 55 to 64 pounds.

Similar general rhizome patterns will be shown to be common among other tall grasses. When one considers this, his concept of grasses as vertically placed organisms is considerably

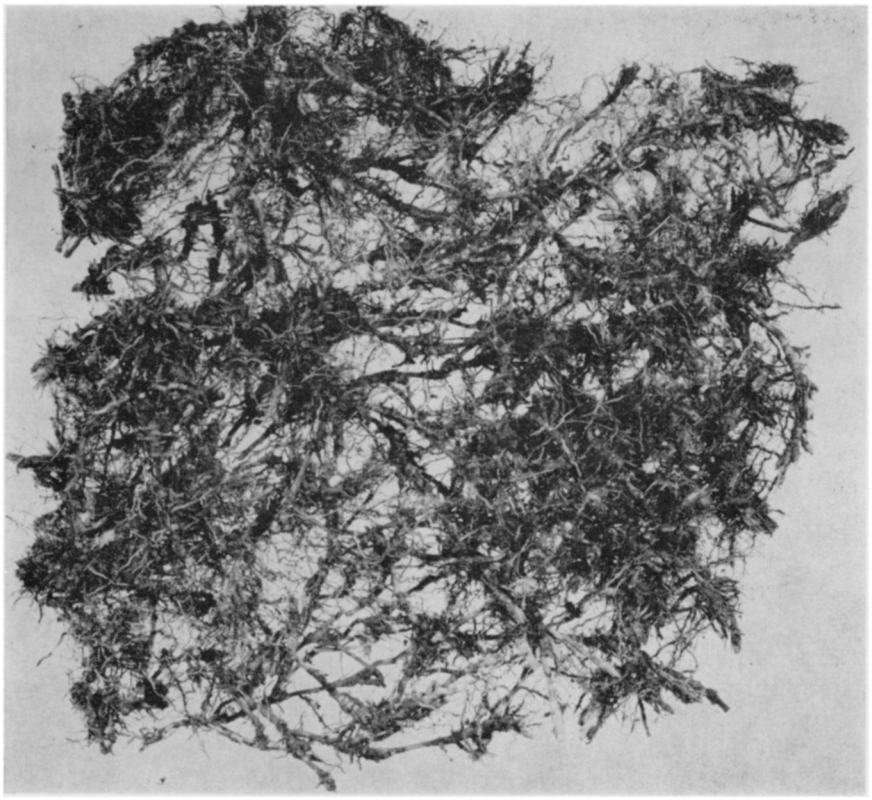

FIGURE 2. Surface view of a square foot of rhizomes of big bluestem after the soil was washed away and roots removed.

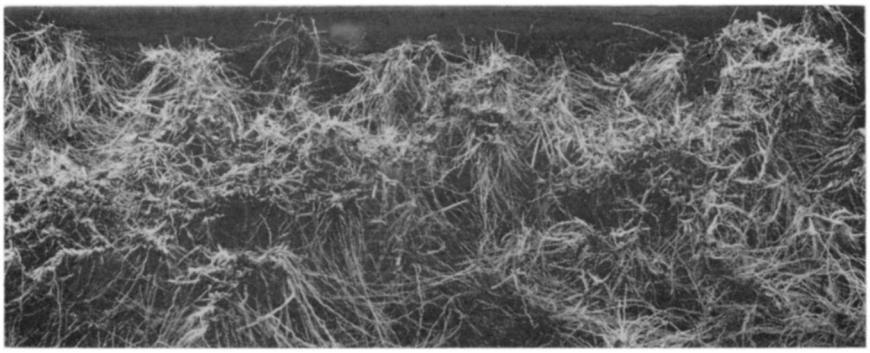

FIGURE 3. Block of big bluestem sod 39 inches long, 20 inches wide and four inches deep from the flood plain of the Missouri River. Rhizomes are anchored by many strong, coarse roots.

modified. Although the shoots and stems of big bluestem extend upward five to ten feet and may appear to occupy all the ground, actually the plant cover (basal area) just above the soil is only about 15 percent (Weaver and Fitzpatrick 1934).

Indian grass

Indian grass *(Sorghastrum nutans)* is a tall, coarse plant with ecological requirements and distribution pattern very similar to that of big bluestem. It may form patches of sod or occur in bunches intermixed with big bluestem, but it is far less abundant. Its usual percentage in western true prairie is only one to five but in the Flint Hills southward it may compose much more of the plant cover.

This grass is slower in producing tillers and rhizomes than most of its competitors, and does not spread so rapidly. Under severe competition tillering is almost nil, a fact which may account for the occurrence of single stems or isolated small bunches scattered among other species. It does seed readily and thrives in disturbed places. The stem bases are nearly as coarse as those of big bluestem but the rhizomes are mostly smaller and shorter. The rhizome mat is shallowly placed. Most rhizomes curve downward and outward two to three inches from the parent stem and then turn upward with very little spreading.

In one square foot of sod there were 58 feet of rhizomes. When air dried they weighed 89 grams. Another sample yielded 48 feet of the short, typically curved rhizomes. This rhizome habit seems much less efficient, as regards propagation, than that of big bluestem.

Switchgrass

Switchgrass *(Panicum virgatum)* grows in wetter soils than big bluestem. Clumps three to five feet in width often occur but this grass is found only infrequently in extensive pure stands. The coarse stems are four to seven mm in diameter but mostly widely spaced. They originate underground at a depth of one to two inches. Switchgrass does not tiller so readily or as abundantly as big bluestem. Owing to lack of basal shoots and wide spacing between unbranched stems, it usually occupies only about five percent of the soil surface even in excellent stands.

A dense network of entangled, somewhat woody and much branched rhizomes is developed. These are three to seven mm thick and one to two feet long. They occur usually at depths of two to five inches but are sometimes eight inches deep. They enable the plant, once established, to spread readily. There are often five to eight internodes per inch of rhizome; branching is frequent and rebranching recurs again and again to form irregular patterns. Often several rhizomes develop from a single base. From these and stem bases a multitude of strong, coarse, poorly branched roots arise. They are thickest around the swollen stem bases but are also scattered along the entire length of the rhizomes. Many extend almost vertically downward about eight feet. Rhizomes occurred at the rate of 43 feet per square foot.

Figure 4 is a view of the rhizomes in an inverted block of sod two feet long and eight inches deep from the Missouri River flood plain. The soil has been

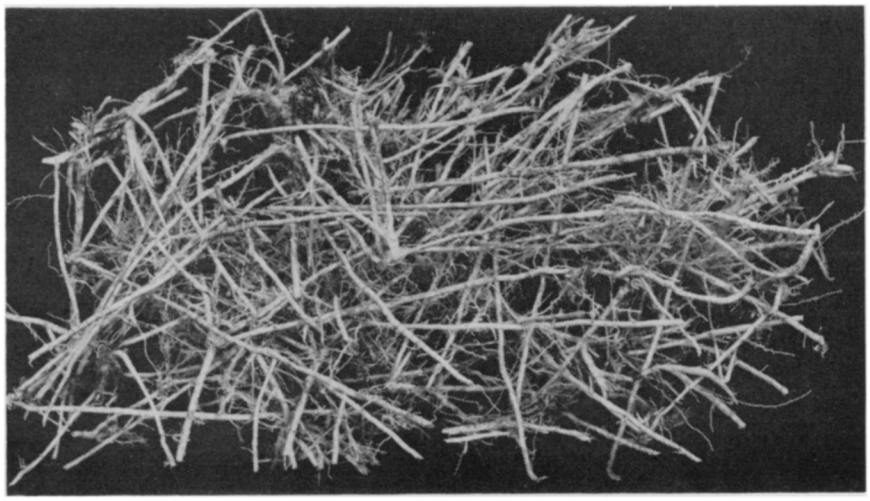

FIGURE 4. Coarse rhizomes on the bottom of an eight-inch-thick mat of the underground framework of switchgrass on a flood plain near Hamburg, Iowa. Under each square foot of soil there were 50 feet of rhizomes.

washed away and nearly all of the roots removed. This vast network extended to within two inches of the soil surface. Each of two square foot samples contained 50 feet of rhizomes. Each sample weighed approximately 192 grams. Another sample from the same area yielded similar results.

The tensile strength of these rhizomes is very great. This was ascertained by placing individual pieces in a tensiometer. The weakest broke only under a pull of 80 pounds and one resisted a pull up to 132 pounds. The volume of 50 feet of four-mm rhizomes was 11.7 cubic inches. Thus, each square foot of the tall-grass sod, whether bluestem or switchgrass, has ample space for food storage. This is reflected in their very rapid growth in spring.

Prairie cordgrass

Prairie cordgrass *(Spartina pectinata)* occupies soil too wet and too poorly aerated for the development of big bluestem and switchgrass. It is a coarse grass, often six to eight feet tall. The stiff woody stems are sometimes ten mm in diameter but so widely spaced that they rarely occupy more than one to three percent of the soil surface. It formerly clothed thousands of acres of low, wet prairie land. Beneath mature plants the soil to a depth of six to ten inches contains a mat of coarse, woody, very much branched rhizomes four to eight mm in diameter. When young they are sheathed with hard, pointed scales which are somewhat longer than the internodes. They vary greatly in length, some exceeding two feet and many extend outward from their origin two to 18 inches before giving rise to erect shoots. The long sharp-pointed buds are well adapted to penetrate heavy, compact soil.

Some rhizomes occur 0.5 to one inch below the soil surface. The elaborate network occupies mostly the upper four inches of soil, but some rhizomes may occur at depths of eight to ten inches, especially where soil is being deposited. Lateral branches originate at various depths from vertically placed rhizomes. Two to several centers of stem bases may be connected by a single rhizome. The golden yellow underground stems are woody but flexible, of very great tensile strength, and intricately intertwined to form an open framework. Individual rhizomes resisted a pull of 46 to 55 pounds before breaking. The network of rhizomes is further anchored by the coarse, deep wire-like roots which arise at stem bases and all along the underground stems.

The rhizomes of a sample from a young stand occurred at the rate of 80 feet per square foot and weighed 124 grams. Those from a long-established stand had a length of 87 feet per unit area and a weight of 208 grams. A third from another wet prairie had 74 feet of rhizomes and a weight of 123 grams. Compared with big bluestem the rhizomes are much coarser and the network more open but greater in the vertical dimension.

Other Lowland Grasses

The coarse, woody mass of rhizomes and roots of eastern gama grass *(Tripsacum dactyloides)* in the surface four inches of soil had twice the weight of that of prairie cordgrass and three times that of big bluestem taken from the same prairie. Reed canary grass *(Phalaris arundinacea)*, like most species from moist lowlands, renews growth in early spring from a vast system of coarse, deep, tangled rhizomes. Redtop *(Agrostis alba)* and saltgrass *(Distichlis spicata)* have extensive systems of rhizomes. But all of these and indeed all combined are of minor importance when compared with the four great dominants described.

Little bluestem

On uplands the dominant species of grasses occur mostly in the bunch form. Usually rhizomes are absent or not well developed. A sample of the compact base of a bunch of little bluestem, *(Andropogon scoparius)* occurring entirely in the surface four inches of soil, is shown in Figure 5. It is three years old and the sod is about eight by ten inches in size. The numerous stem bases, the very short rhizomes, and the hundreds of roots are securely knit together into a somewhat circular clump. Although the individual

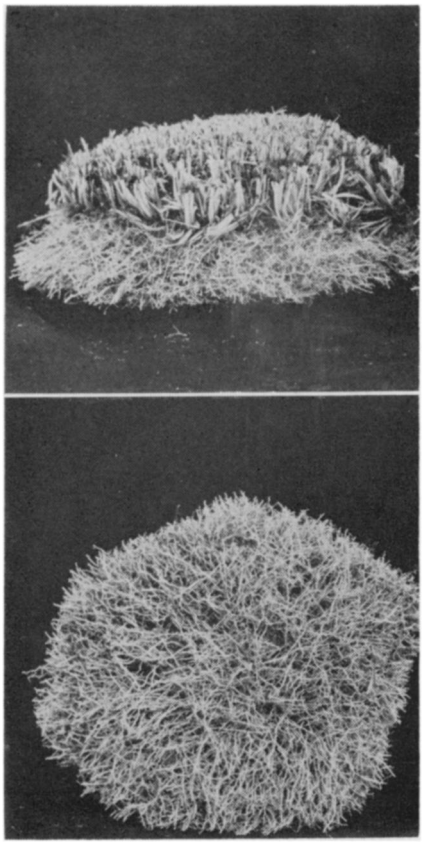

FIGURE 5. (Above) Sod formed by little bluestem includes stem bases and roots. (Below) Upturned sod showing abundance of fine roots.

rhizomes rarely exceed an inch in length, their total length according to Mueller (1941) may be 300 feet per square meter. This block of sod could not be broken or pulled apart by hand, and it was cut only with a sharp

spade. It was securely held in place by a deep network of strong roots. Since, according to Pavlychenko (1942), a single root has a tensile strength of about 2.5 pounds, one can only marvel at the wonderful way in which the plant is anchored to the soil.

In good stands 15 to 20 bunches often occur in an area of ten square feet with diameters near the soil surface of four to eight inches. The spread of the foliage, however, is two to three times that of the basal area. In deep soils on the drier hillsides this species alone frequently furnishes 90 percent of the vegetation and in drier soils as a whole, including nearly level uplands, 55 to 75 percent. The average basal cover in the little bluestem community rarely exceeds 25 percent and is usually about 15. Little bluestem alone, on an average, occupies ten percent of the soil surface.

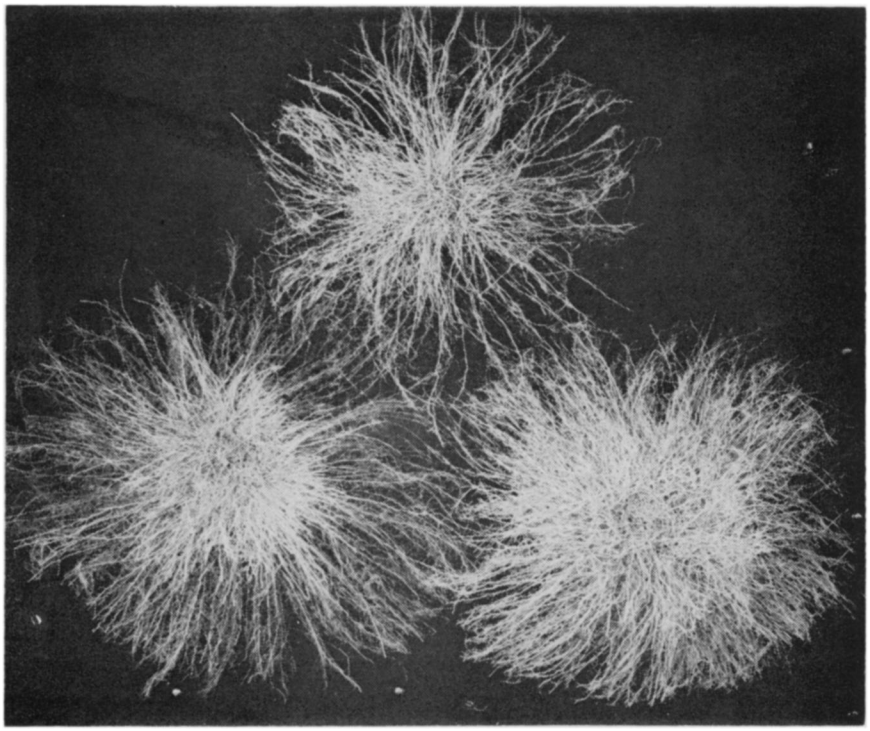

FIGURE 6. Basal view of bunches of prairie dropseed (lower left), tall dropseed (lower right), and needlegrass. Only the roots in the surface four inches of sod are shown.

It has long been believed that the earlier death in drought of little bluestem compared with big bluestem was due to the deeper root system of the tall grass. This usually exceeds that of the mid grass by one to two feet. Further study indicates, however, that accumulated food supply in the sod, which is much greater in big bluestem, may also have been an important factor in survival.

The roots of bunch grasses extending far outward from the base of the plant are so important in the formation of sod that they should be well understood. This habit is very similar in needlegrass *(Stipa spartea)*, prairie dropseed *(Sporobolus heterolepis)* and others to that of little bluestem.

In Figure 6, blocks of sod were taken to include the soil eight inches on all sides from the center of the bunch. The sod was then cut at a depth of exactly four inches. After long soaking in water the soil was washed away, thus exposing the roots that extended outward on all sides of the bunches. The bunches varied in diameter from two inches (needlegrass) to 4.5 inches (prairie dropseed). These roots were all in the 1.5 to four inch soil level. In washing, all other plant materials were separated from the roots and discarded. Roots arising from the vertical bases of buried stems spread outward in all directions, many crisscross under the bunch and extend outward on the opposite side. Most of the roots, however, grow more or less vertically downward, but some from all of these grasses extend outward at least two feet in the upper four inches of soil (Weaver 1958).

A plot of little bluestem sod of about six square feet (35 x 25 in.) is shown in Figure 7. The larger bunches are little bluestem except one in the left background which is Indian grass. Two small plants of needlegrass are shown (central left) and two of Junegrass *(Koeleria cristata)* in the background. Only the stem bases and roots occurring in the upper four inches of soil are shown. Thus, one to 1.5 inches of stem bases are found just below the soil surface.

Surrounding the compact bunches of grass stems, with roots three to five feet deep in prairie soil, is a vast network of intermingled fibrous roots, each of great tensile strength, which hold the soil against erosion by wind and water. The content of the surface two inches of soil between the bunches, as regards amount of plant material, must also be considered. Numerous samples of the surface two inches of sod were taken between the bunches. The interspaces selected were free from half-developed bunches or coarse forbs. The numerous blocks of sod were trimmed before soaking to exactly one square foot and two-inch depth. All debris and dead organic mulch was then removed and the plants

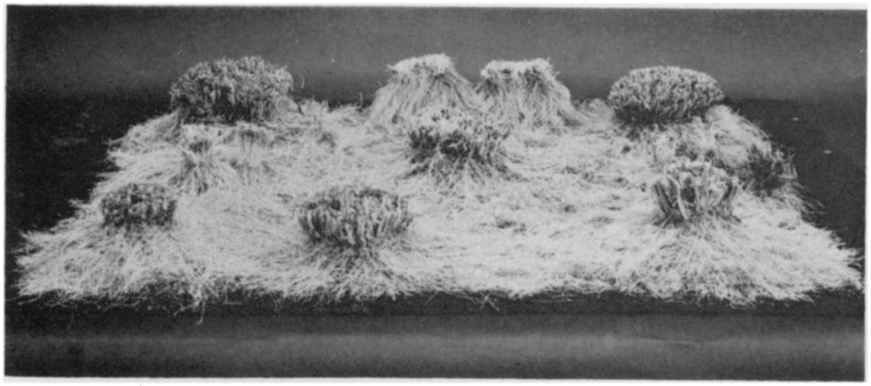

FIGURE 7. Plot of little bluestem prairie showing stem bases and roots in surface four inches of soil.

clipped to the soil surface. The soil was then removed by washing; the mats of roots and rhizomes were air dried and weighed.

Species in the interbunch sod were numerous but the plants were small. Weight per square foot averaged 28 grams. This indicates that more than one ton per acre of plant material occurs between the bunches of dominant grasses of upland.

The weight of the mass of roots and stem bases, after all soil was removed and the plant materials air dried, has been obtained from 16 prairies in western Iowa, eastern Nebraska, and central Kansas. It was 3.15, 2.60 and 2.34 tons per acre respectively, the amount decreasing westward somewhat in proportion to rainfall (Shively and Weaver, 1939). Thus, the main cause of the great stability of upland prairie soil is found in the solidly anchored bunch grasses and the interlocking of the surface tangle of their wire-like roots between the bunches. This is reinforced by roots and rhizomes of plants growing between the bunches. Perusal of the preceding facts leads one to agree with Clements (1938) that "during the historical period, dust storms have come only from soils exposed by man in the course of settlement."

Other Grasses and Grass-like Plants

Many grasses and sedges of uplands are provided with rhizomes. Scribner panicum *(Panicum scribnerianum)* a small perennial, occurs almost everywhere in prairie and propagates by means of short rhizomes. Sideoats grama *(Bouteloua curtipendula)* produces scaly rhizomes two to five inches long. Kentucky bluegrass *(Poa pratensis)* is a constant but small component (about five percent) of prairie. Rhizomes are 0.5 to two mm. in diameter and some are five to 12 inches long. A single square foot of sod may contain 60 or more feet of rhizomes. Moreover, big bluestem commonly forms five to 20 percent of upland vegetation.

Certain sedges range widely throughout upland prairie. Their rhizomes contribute considerably to soil stability. Penn sedge *(Carex pennsylvanica)* is the most widely spread and very locally may form half of the plant cover. Meads sedge *(C. meadii)* produces yellowish-brown, shallow rhizomes about five mm thick. They are long but not much branched and usually connect several plants. A single square foot of sod contained 102 feet of rhizomes.

A most remarkable invasion by rhizomes was exhibited by western wheatgrass *(Agropyron smithii)* during the great drought of the thirties. It occurred only sparsely in true prairie but great losses sustained by the bluestems and other grasses and the bare areas thus produced made possible its enormous spread. It often became the most abundant grass to within 40 miles of the Missouri River. In addition to being a good seed-producer, large, more or less circular areas where other grasses were nearly dead indicated the excellent and rapid method of migrating by long, much-branched rhizomes (Figure 8). The vitality of the rhizomes and their resistance to drought are remarkably great. The boundaries of spreading patches of wheatgrass were marked in many places and a yearly advance by rhizomes of nine to fourteen feet was ascertained.

The long slender rhizomes are one to three mm in diameter, glistening white when young but straw-colored when mature. They vary in length from a few inches to five or more feet. A

FIGURE 8. Invasion of western wheatgrass into big bluestem sod. The soil was washed away revealing the dead underground parts of the former dominant (black) and the shining white rhizomes of wheatgrass.

single plant may develop several rhizomes of great tensile strength. They are much branched into a coarse, tangled network, which with the stem bases and abundant tough roots form a sod between depths of 1.5 and five inches. But in drifting, wind-blown soil they may be 12 inches deep, yet some shoots from them may reach the surface soil. The mass of rhizomes and roots in the sod of old stands is only about an inch thick. Total length of rhizomes per square foot in such stands was 84 feet. Wheatgrass is not a good competitor under normal true-prairie environment and is now about as rare as before the great drought.

Summary

Big bluestem produces great numbers of branched rhizomes, three to nine mm in diameter, compacted into dense mats about two inches thick at depths between one and three inches. Their length per square foot of sod averaged 55 feet. Tensile strength was 55 to 64 pounds for individual rhizomes. Indian grass is similar to the preceding grass in total length of rhizomes and their position in the sod, but it is less efficient in spreading.

Switchgrass has rhizomes three to seven mm thick and one to two feet long. It differs from big bluestem by forming an open framework two to five inches, but sometimes eight inches deep. A square foot of soil contains about 50 feet of much branched and interwoven rhizomes. A single rhizome exhibited a tensile strength of 80 to 132 pounds.

Beneath mature plants of prairie cordgrass the soil to a depth of six to ten inches contains a mat of coarse, woody, much branched rhizomes four to eight mm thick. Lateral branches originate at various depths from vertically placed rhizomes. Some exceed two feet in length and lateral spreading is rapid. Compared with big bluestem the rhizomes are much coarser and the network much more open, but greater in the vertical dimension. Total length of rhizomes averaged 80 feet per square foot. On moist lowland rhizomes are common on many grasses, sedges and rushes.

Of the rhizome networks of the four chief lowland grasses, that of big bluestem is the shallowest. That of Indian grass is very similar in the vertical dimension. Switchgrass forms an open network with a depth of three to eight inches. Prairie cordgrass has a framework of variable thickness, ranging from two to eight inches.

Rhizomes furnish abundant room for storage near the food factories above and they are close to the water and nutrient supplies around and beneath them. Fifty feet of rhizomes with an average diameter of four mm have a volume of 11.7 cubic inches. Above these food-storage reservoirs the tall coarse grasses rapidly develop shoots, followed by an enormous expanse of leaves.

Dominants of uplands are mostly, but not all, bunch grasses. The most abundant of these is little bluestem. Its compact bases are closely compressed in the surface 1.5 to two inches of soil. Roots arise from the bases of buried stems and spread outward in all directions, thus binding the stems together and firmly anchoring the bunch. Roots spread laterally in great numbers to at least two feet in the surface four inches of soil. Numerous other plants, especially other grasses, grow between the large bunches and also occupy a part of the upper soil. Their roots and rhizomes furnish a considerable part of the 2.6 to 3.15 tons of plant materials per acre in the upper four inches of soil—the bluestem sod. This is essentially true of bunches of prairie dropseed and needlegrass, which also maintain upland communities.

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